The relative importance of food biomass and quality for patch and habitat choice in Brent Geese *Branta bernicla*

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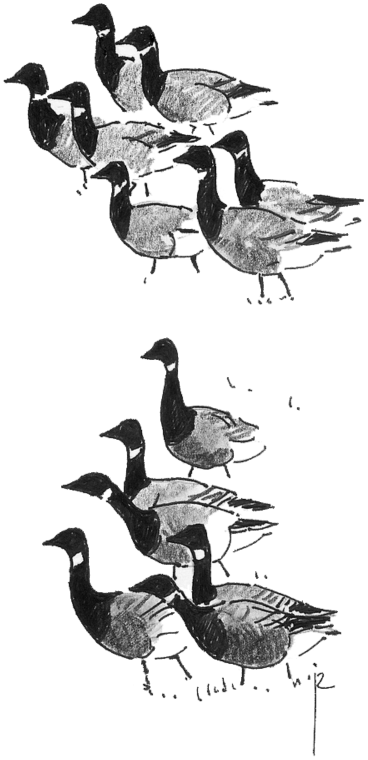

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We studied the relative importance of food biomass and food quality for habitat preference in Brent Geese *Branta bernicla* by experimentally manipulating forage parameters. Levels of biomass and food quality (nitrogen content) were independently enhanced in plots of 2 x 6 m by temporary exclusion from grazing and addition of artificial fertiliser in a full-factorial experiment. Preference was quantified by bird density, grazing pressure and interaction frequency. Instantaneous intake rate increased linearly with sward height over the range studied. Wild-ranging Brent Geese preferred plots with the highest nitrogen content. These results complement earlier work (Riddington *et al.* 1997, Hassall *et al.* 2001, Durant *et al.* 2004) by demonstrating that food quality is an important parameter determining patch choice and is acting at all biomass levels. Our results support the expectation that patch choice is influenced by nitrogen intake rates. This provides an explanation for distribution patterns of Brent Geese on agricultural grasslands, and the sequence in which pasture and marsh habitats are utilised in spring.

Key words: food preference – grazing waterfowl – nitrogen – intake rates – feeding strategies

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INTRODUCTION

Classical foraging theory centres on forage biomass as the crucial determinant for patch choice (Spalinger & Hobbs 1992, Gross *et al.* 1993, Ginnett & Demment 1995). It predicts for plant-herbivore systems that herbivore density reaches its maximum at the highest forage biomass (Oksanen *et al.* 1981). This generalisation does not fit the empirical facts, however, as grazing pressure of herbivores observed in the wild is often highest at intermediate biomass. Fryxell (1991), and later van de Koppel *et al.* (1996), provided a theoretical framework to account for the effect of food quality on resource acquisition in herbivores. Fryxell (1991) showed that aggregation of ruminants at intermediate levels of biomass can result from spatial variation in food quality and from forage maturation effects, assuming that food quality declines with increasing biomass. Experimental work by Langvatn & Hanley (1993) and Wilmshurst *et al.* (1995) on Red Deer *Cervus elaphus* supports the model prediction that intermediate amounts of biomass are preferred over patches with high biomass, if the intake rate of energy or protein is higher in the first.

The average quality of the diet is negatively related to body size in mammalian (Prins & Olff 1999) and avian (Van Eerden 1997) herbivores. Small herbivores, such as lagomorphs and herbivorous waterfowl, are therefore more likely to be affected by differences in food quality than large ruminants. In waterfowl, food is poorly digested due to a relatively short digestive tract and high passage rates (Prop & Vulink 1992). This makes them more sensitive to food quality than expected according to body size (Sedinger 1997). Geese, for example, typically feed on high quality food (Owen 1980). Indeed, many field studies show relationships between foraging decisions of waterfowl and food quality: at the diet level, geese choose those components that yield the highest energy and protein intake rate (Prop & Deerenberg 1991). At the patch level, geese select food containing a high nitrogen content (Ydenberg & Prins 1981, Teunissen *et al.* 1985, Vickery *et al.* 1994). And similarly at the large scale of staging sites habitat choice is related to protein content (Boude-wijn 1984, Prins & Ydenberg 1985). In many of these examples, however, the analysis is confounded by differences in plant production, biomass and, presumably, the intake rate of food. It is therefore difficult to determine to what extent foraging decisions are affected by intake rate or by the quality of the food.

Riddington *et al.* (1997) and Hassall *et al.* (2001) showed the importance of nitrogen for patch choice in Brent Geese *Branta bernicla bernicla*. In their study with wintering Brent Geese on coastal grasslands in Britain, birds preferred short swards over tall, unfertilised swards, due to a negative correlation between nitrogen content and sward height. Fertilisation resulted in a preference for tall swards. They explained their findings by arguing that swards of intermediate length are preferred due to opposing constraints associated with sward height (the forage maturation hypothesis). At low sward heights intake rate forms an important constraint, while nitrogen content and digestive constraints become important at taller swards.

We elaborate upon their concept by manipulating the same parameters under different circumstances. Our study focuses on the spring situation, when swards are generally short. At that time of the year, birds are also in a different physiological state than in winter, as they have to acquire fat reserves for spring migration and breeding (Ebbinge & Spaans 1995). Following Riddington *et al.* (1997) and Hassall *et al.* (2001), we started from the premise that both food quality and biomass affect patch choice and that intake rate is positively related to biomass. We studied the relative importance of these variables by experimentally manipulating both food quality and biomass. Patch choice was estimated from grazing pressure as well as from behavioural measures for wild Brent Geese, and we established the relationship between biomass and intake rate of food using captive animals. After McKay *et al.* (1994) and Hassall *et al.* (2001), who stressed the importance of protein acquisition for Brent Geese, we used nitrogen content as a measure of quality in our study.

STUDY AREA

The experiment was carried out at the cattle-grazed salt marsh (400 ha) of Schiermonnikoog (53°30'N, 6°10' E), a barrier island in the Dutch Wadden Sea. In spring, numbers of Brent Geese staging on Schiermonnikoog range between two and four thousand (Bos & Stahl 2003). For a detailed description of the salt marsh see Olff *et al.* (1997). In early spring the geese spend most of the time foraging in the embanked polder (270 ha), but towards May a gradual shift to the salt marsh is observed. Barnacle Geese *Branta leucopsis* are also important herbivores utilising the marsh (Prins & Ydenberg 1985), leaving the island at mid-April (Bos & Stahl 2003). Although European Brown Hares *Lepus europaeus* are abundant at some of the ungrazed sites, their density at the cattle-grazed salt marsh was relatively low during the experiments (hare grazing pressure: 0.02 ± 0.01 droppings m^{-2} d^{-1}, mean ± SE for control plots of own experiments; see also Kuijper 2004). The salt marsh is grazed by cattle from the end of May until November at a stocking rate of 0.5 cow ha^{-1} and harbours a mosaic of plant communities (van Wijnen *et al.* 1997). The plant communities characterised by Red Fescue *Festuca rubra* and Common Salt-Marsh Grass *Puccinellia maritima*, experience the highest grazing pressure by Brent Geese in May when compared to the rest of the island marsh (Van der Graaf *et al.* 2002).

METHODS

We selected 28 plots (or patches) of 2 x 6m within the Juncetum gerardi and the Puccinellietum maritimae plant communities, on the cattle-grazed salt marsh. The communities were dominated by a short sward of Red Fescue (41% cover), Salt Rush *Juncus gerardi* (20% cover) and Common Salt Marsh Grass (15% cover), and were frequently visited by Brent Geese. The plots were homogenous with respect to vegetation composition and height. Subdivision into 7 replicate blocks of 4 plots each was made, where plots within a block were closer to each other than to plots in adjacent blocks. Average distance between plots within a block was approximately 4 m. Four different treatments were assigned randomly to each plot within a block. These treatments consisted of fertiliser application and temporary herbivore exclusion in a full-factorial design. This resulted in plots of high quality with high biomass (fertilised & exclosed, FE), low quality and high biomass (unfertilised & exclosed, UE), high quality and low biomass (fertilised & grazed, FG) and finally low quality with low biomass (unfertilised & grazed, UG). Fertilisation was accomplished using a commercial fertiliser ($CaCO_3.NH_4NO_3$, 27%), dissolved in water and sprayed over the vegetation, resulting in an addition of 25 g of N m^{-2}. Geese and hares were excluded for 3 – 4 weeks using chicken wire (5 cm mesh width, 50 cm high). The experiment was carried out in two spatially separated series where plots of each series were matched for homogeneity of the sward and arranged within sight of an observation hide. The first 3 complete blocks (12 plots) received the treatments on 1 April 1998. The second series of 4 blocks (16 plots) was treated on 5 April. An observation tower was placed within a distance of 100 m from the plots and behavioural data of the geese were recorded, starting from the moment that the exclosures were removed. Observations started on 22 April and 5 May for the first and second series respectively.

Vegetation analysis

The day before the exclosures were removed, the sward height and the available biomass were measured. Sward height was measured with a 24 g polystyrene disc (20 cm diameter) that was dropped on the vegetation, sliding along a calibrated stick that rested on the ground. Aboveground biomass was estimated by randomly cutting one sod of 10 x 10 cm per plot to ground level in order to calibrate our measure of sward height. The material was sorted into live and dead material, washed, dried at 60°C for 48 hours and weighed. In addition to that, reflectance values were measured for red and infra red light using a PSII field spectrometer (ASD, Boulder), and an index of green biomass was calculated (Normalised Difference Vegetation Index, or NDVI (value), cf. Esselink & van Gils 1985). Sward height was linearly related to the biomass of green leaves (g dry mass m^{-2}; $y = 0.099 + 0.32x$, $r^2 = 0.84$, $P < 0.001$) and to the green biomass index ($y = 0.68 + 0.048x$, $r^2 = 0.42$, $P < 0.001$). The development of live standing biomass over time was monitored by measuring the green biomass index at weekly intervals. This method is suitable to detect small differences in the availability of green biomass and can be taken repeatedly without physical disturbance to the experiment. On a more detailed scale, growth and depletion were measured using the leaf length of individually marked Red Fescue or Common Salt-Marsh Grass tillers following Bakker & Loonen (1998). For this purpose 18 tillers were selected per plot in 4 of the blocks and their leaf lengths measured every six days. Leaf elongation was estimated from ungrazed tillers only. On the basis of these measurements on individually marked tillers, the percentage of grazed leaves was determined for each plot. Data were recalculated as percentage of leaves grazed per day. Vegetation composition was recorded for entire plots by visual cover estimates of plant species following Londo (1976).

A mixed sample of the green leaf tips of Red Fescue and Common Salt-Marsh Grass, and a sample of Salt Rush was taken from each plot, weighed and stored in a transport box containing ice. Samples were stored at –80°C within 12 hours after collection until later analysis of total nitrogen concentration (following a modified Kjeldahl method).

Foraging behaviour of Brent

The experimental plots were observed from dawn to dusk. Goose densities and number of agonistic interactions were recorded at regular intervals by sequentially scanning each plot and observing it for ten seconds (see Teunissen *et al.* 1985). An agonistic interaction was defined as a sudden interruption of the current behaviour of an individual to chase another. Interaction frequency (n bird $^{-1}$10 sec^{-1}) was assessed by dividing the number of interactions by the number of birds present in the plot. Average bird density was calculated by dividing the total number of birds observed in each plot by the frequency with which at least one goose in that particular block was counted. Visit time (bird minutes) was calculated by multiplying the amount of time that geese were present in a plot with the average hourly bird density in the plot. We collected data on step and peck rates per plot at regular intervals for as many individual animals as possible. Step and peck rates were determined by measuring the time required for 10 steps and 50 pecks respectively using a chronometer. At regular intervals, droppings were counted on the entire experimental plots and removed. Grazing pressure was defined as the number of droppings per unit area per day.

Instantaneous intake rate of food was estimated using a pair of captive Brent Geese in an experimental chamber at the laboratory. These geese were allowed to eat 50 pecks from a sod of 10 x 20 cm. Sods were taken from the plots of the field experiment on the day prior to opening of the exclosures to wild geese and weighed before and after the trial to the nearest 10 mg (Sartorius pro 32/34F). Removed biomass (W_r, g fresh weight) was measured as the weight loss of the sod during the trial, corrected for spilled food and evaporation. Evaporation rate (g s^{-1}) was estimated from the weight loss of the same sod in the same room, during five minutes prior to the trial, and multiplied by the duration of the trial to arrive at evaporation. Time spent pecking per individual (T_p, s) was measured using video recordings. The intake rate (g fresh s^{-1}) was calculated as W_r / T_p. Sods were provided to the geese in random order, with an interval of 20 min. During the experimental trials and the 8 weeks before, the geese were housed in a 2 x 2 m indoor facility and additionally fed with dried food pellets and grass presented as sods. Light regime followed outdoor conditions. The geese had been captured from the wild in 1996 and had been housed in a large open aviary until 8 weeks before the experimental trials. All catching, handling and non-invasive experimentation with captive geese in this study was conducted under a permit from the Dutch Ministry of Agriculture, Nature Manage-ment and Fisheries and a DEC permit of the University of Groningen (DEC No BG07696).

Data analyses

Data were averaged per plot to avoid pseudo-replication and analysed using a Randomised Block ANOVA (Zar 1996). In this analysis ‘fertilisation’ and ‘grazing’ were entered as fixed factors and ‘block’ was entered as a random factor. When appropriate, data were square root transformed. Percentage values were arcsine transformed. Post-hoc comparisons between the four treatments were carried out using Tukey’s honestly significant difference test. When the assumptions of parametric ANOVA could not be met, a non-parametric Friedman ANOVA and associated post-hoc comparisons (Zar 1996) were used instead. Changes in peck and step rate over time were investigated to study depletion effects. Here, a multiple linear regression was carried out, with treatment as a factor and time (cumulative hours of observation after start of the experiment) as a covariate. The foraging parameters peck rate, step rate and intake rate were related to vegetation height, nitrogen content and the interaction between them, using backward multiple regression, eliminating variables when they were not significant at the 0.05 level. Finally, we used bird density, interaction frequency and grazing pressure as parameters of preference and tested for the effect of vegetation height, nitrogen content and the interaction between them, using backward multiple regressions. In these regression analyses we corrected for differences between the two series by incorporating series as a fixed factor. Statistical analyses were carried out with SPSS 11.5.

RESULTS

Treatment effect on the vegetation

At the start of the observations a significant difference in total live biomass was found between exclosed plots (UE, FE) and those that had been grazed (UG, FG; $F_{1,18} = 12.4$, $P < 0.05$. Other indices of food biomass, the green biomass index and sward height revealed the same pattern (Table 1). Parameters of food quality were also strongly related to the treatments. Food plants in fertilised plots (FG, FE) had a higher nitrogen content ($F_{1,18} = 130$, $P < 0.001$) than plants in unfertilised plots (UG, UE). A significant interaction ($F_{1,18} = 10.7$, $P < 0.05$) between fertilisation and grazing arose as the nitrogen content was enhanced by grazing in unfertilised plots. No differences in plant species abundance were observed between the treatments.

Behavioural parameters and grazing pressure

Total visiting time per plot increased over time, although at different rates for each treatment (Fig. 1 A, B). Fertilised treatments had higher bird densities ($F_{1,18} = 28.4$, $P < 0.001$, Table 1) and received higher grazing pressure ($F_{1,18} = 93$, $P < 0.001$). The percentage of leaves grazed of Common Salt-Marsh Grass and Red Fescue in the different treatments were closely related to grazing pressure (Table 1). The frequency of agonistic interactions did not differ between treatments. Previous exclusion of grazing had no significant effect on bird density, number of interactions and grazing pressure.

Fertilisation had a significant effect on step rate of geese (Table 1); with increasing nitrogen content of the grasses, the step rate decreased ($r^2 = 0.33$, $P < 0.01$). Peck rate was not affected by any of the treatments. Neither peck, nor step rate changed significantly over the course of the experiment. Instantaneous intake rate increased linearly with biomass ($F_{1,14} = 55.2$; $y = 0.045x - 0.00043$, $r^2 = 0.792$, $P < 0.001$, Fig. 2). This is mainly due to an increase in bite size with increasing levels of biomass (data not shown). Nitrogen content was not important in explaining variation in intake rate.

Case histories of individual patch choice

In three cases during the first series of observations, we were able to follow specific family units for some time. The birds were recognisable by their behaviour and from family composition, and monopolised plots for substantial time periods. One plot, the second replicate of the FE treatment, was initially occupied by a paired, aggressive male. This male threatened other birds at a distance up to 10 m, and effectively monopolised the plot for more than three hours. The plot was taken over after a fight by a family with three young which had spent 15 minutes at the FG plot immediately before. This family maintained control over the plot for two hours, after which all birds in the area departed due to a disturbance. Both the pair and members of the succeeding family had short excursions to adjoining plots with different treatments. These excursions never lasted longer than 2 minutes. Another family with three juveniles occupied a FE plot for periods of more than two hours during both observation days.

Table 1. Mean values of sward and foraging parameters for different treatments. Test results for the effect of manipulation by grazing and fertilisation are indicated by the following abbreviations: F = fertilisation, G = grazing, FxG = interaction between fertilisation and grazing. Levels of significance are indicated using asterisks: * = 0.05, ** =0.01 and *** = 0.001. RB refers to a non-replicated randomised block ANOVA and F refers to Friedman ANOVA. Different letters (a, b) indicate significant differences between treatments (post-hoc tests). Sample sizes for leaf elongation, % of leaves grazed, and intake rate deviate from the maximum value of 28 as these parameters were only determined for the second series of measurement. Sample sizes for foraging parameters vary as not all plots were visited by geese.

		Unfertilised				Fertilised								
		Grazed		Ungrazed		Grazed		Ungrazed						
Sward characteristics	*n*	*UG*	*SE*	*UE*	*SE*	*FG*	*SE*	*FE*	*SE*	Test	F	G	FxG	Block
Sward height (cm)	28	1.8	0.1^a	3.0	0.2^b	1.6	0.1^a	3.8	0.3^c	RB	ns	***	*	ns
Vegetation index (value)	28	0.76	0.03^a	0.81	0.02^{ab}	0.76	0.02^a	0.89	0.01^b	RB	**	***	**	***
Cover of *Juncus gerardi* (%)	28	18.9	4.2	27.9	8.4	16.1	3.6	17.9	4.9	RB	ns	ns	ns	ns
Cover of grasses (%)	28	55.6	3.7	52.5	8.3	55.9	4.9	60.6	5.7	RB	ns	ns	ns	ns
Nitrogen content (mg g dw^{-1})														
Festuca + Puccinellia	28	31.9	1.5^a	22.3	2.0^b	46.9	2.4^c	49.3	1.2^c	RB	***	ns	*	ns
J. gerardi	21	38.8	2.0^{ab}	30.5	4.0^a	45.8	2.0^{bc}	48.0	1.0^c	RB	***	ns	*	ns
Leaf elongation (mm tiller^{-1}day^{-1})	16	1.4	0.2^a	1.8	0.2^{ab}	1.8	0.7^{ab}	2.5	0.7^b	F				
Foraging parameters														
Peck rate (sec peck^{-1})	22	0.36	0.02	0.39	0.02	0.36	0.03	0.43	0.05	RB	ns	ns	ns	***
Step rate (sec step^{-1})	21	1.7	0.3	1.7	0.1	2.7	0.3	3.7	0.5	RB	**	ns	ns	ns
% of leaves grazed day^{-1}	16	0.8	0.2^a	1.7	0.5^a	5.7	0.3^b	7.5	0.5^b	RB	**	ns	ns	ns
Bird density (n plot^{-1})	28	0.6	0.3^a	0.5	0.2^a	2.4	0.4^b	3.3	0.6^b	RB	***	ns	ns	ns
Interaction frequency (n bird^{-1} 10 seconds^{-1})	22	0.04	0.01	0.06	0.02	0.10	0.01	0.09	0.02	RB	ns	ns	ns	ns
Intake rate (g fresh s^{-1})	16	0.024	0.005^a	0.041	0.007^a	0.030	0.004^a	0.072	0.005^b	RB	*	**	ns	ns
Grazing pressure (droppings m^{-2} d^{-1})	28	0.43	0.11^a	0.55	0.20^{ab}	1.54	0.30^{bc}	2.17	0.60^c	RB	***	ns	ns	***

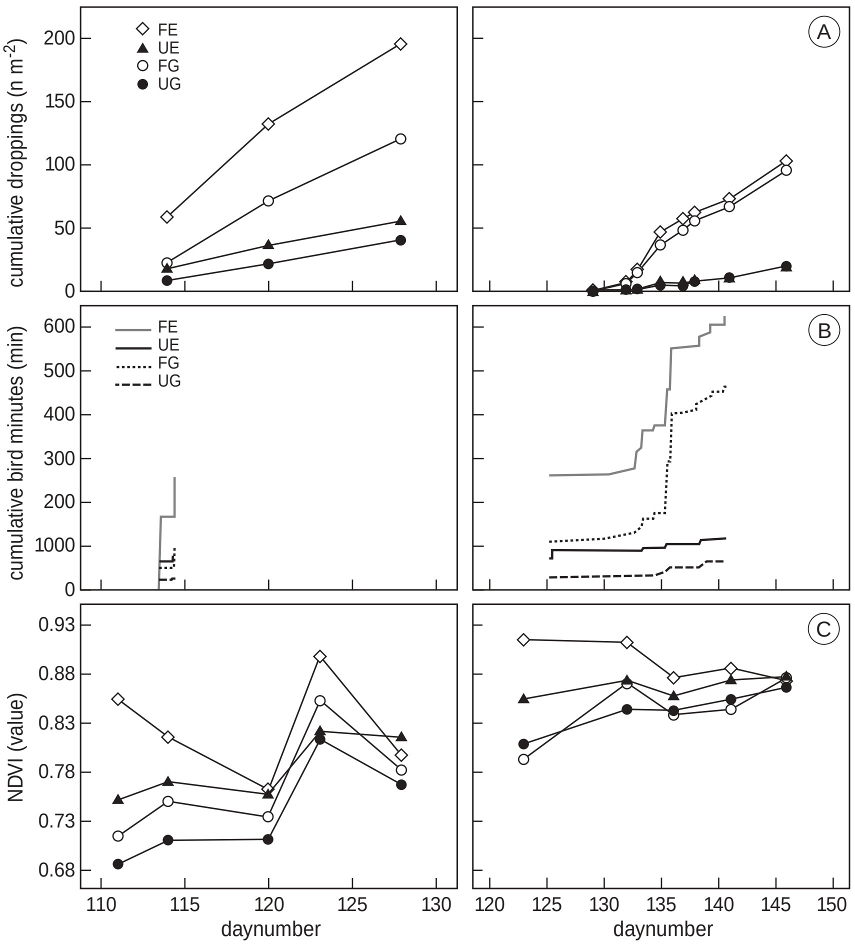

Figure 1. Measures of use by Brent Geese of the experimental treatments over time: (A) Cumulative grazing pressure (droppings m^{-2}). (B) Cumulative visit time (bird minutes) on the plots expressed on an hourly basis. We were able to observe the second series of the experiment for 15 days, but practical reasons limited the observation period for the first series to three subsequent days. (C) Normalised Difference Vegetation Index (NDVI), the ratio of red and infrared light reflected by the vegetation. The left panel refers to the first, the right panel to the second series of the experiment. FE fertilised & exclosed; UE unfertilised & exclosed; FG fertilised & grazed; UG unfertilised & grazed

Plant growth and food depletion over time

Over the experimental period the initial differences in green biomass index between treatments tended to disappear (Fig. 1C), to a large extent because of a decline in aboveground biomass in the fertilised & exclosed plots (FE). Episodes of decline in biomass were apparent in the fertilised treatments (FE, FG), coinciding with periods of grazing, but unfertilised plots (UE, UG) hardly showed such decline because the intensity of grazing was much lower. However, differences in biomass between the grazing treatments remained visible and the rank order of the treatments in terms of biomass-index remained largely the same. There was a parallel increase in grazing pressure (Fig. 1A) and visiting time (Fig. 1B) among treatments. Leaf elongation did not differ between the fertilised treatments (FE, FG) and the unfertilised & exclosed treatment (UE, Table 1).

Preference in relation to biomass and quality

The three parameters of patch preference by geese were related to nitrogen content of the main food species, though the frequency of agonistic interactions only marginally (Table 2). Neither vegetation height nor an interaction between sward height and nitrogen content contributed to explaining any of the variation in patch preference.

Table 2. Multiple linear regression models relating parameters of patch preference to sward height and nitrogen content of the grasses. The two experimental series were included as fixed factor. For all three models the interaction term (vegetation height x nitrogen content) was not significant and excluded from the final models

Grazing pressure $r^2 = 0.58$	*df*	*F*	*P*
Series	1	16.22	< 0.001
Vegetation height	1	0.58	ns
N content	1	14.99	0.001
Corrected model	3	11.03	< 0.001
Intercept	1	2.05	ns
Corrected total	27		

Bird density $r^2 = 0.62$	*df*	*F*	*P*
Series	1	7.59	< 0.05
Vegetation height	1	2.88	ns
N content	1	27.36	< 0.001
Corrected model	3	12.82	< 0.001
Intercept	1	10.16	< 0.01
Corrected total	27		

Interaction frequency[a] $r^2 = 0.35$	*df*	*F*	*P*
Series	1	6.66	< 0.05
Vegetation height	1	0.03	ns
N content	1	3.28	ns (0.09)
Corrected model	3	3.25	< 0.05
Intercept	1	1.08	ns
Corrected total	21		

[a] sample size is lower for this parameter as not all plots were visited; plots without geese were included in the calculation of bird density

DISCUSSION

Patch preference

The experimental manipulations resulted in clear differences in food quality between treatments while plant species abundance was not significantly altered. Fertilised plots had higher values of nitrogen than unfertilised treatments, and likewise the amount of biomass was higher. We found that instantaneous intake rate was linearly related to biomass (Fig. 2), similar to the findings of Hassall *et al.* (2001). With our experimental set-up we break the correlation between biomass and quality as we manipulated both parameters independently, and can now investigate their relative importance for patch preference in small herbivores.

We evaluate three measures of preference. The first measure, bird density, is considered by us as an instantaneous measure, and indicated a preference for fertilised plots (Table 1). The second measure, grazing pressure, provides a measure over a longer period, i.e. a day or more, and showed the same pattern (Table 1). The uniformity in response at different time scales argues against strong short-term effects of depletion or production. Such potential effects were also not detectable from a changing pattern of visits to the treatments over time (Fig. 1A, B), or changes in peck and step rate over time. Depletion therefore does not appear to affect our conclusions. The third measure, the frequency of interactions, shows no differences between treatments. We argue, nonetheless, that our behavioural observations are valuable for the interpretation of the results. Some of the fertilised plots were monopolised by distinct goose families for a longer period. These anecdotal observations support our other indices of preference, as dominant pairs are apparently willing to defend profitable plots. A similar phenomenon was observed

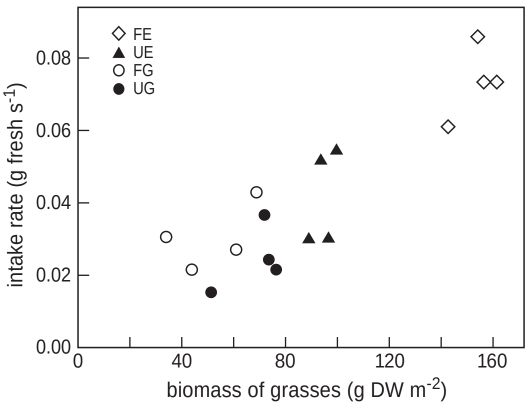

Figure 2. Relationship between intake rate and biomass on offer. Each data point represents the mean of a duplicate measurement.

by Stahl *et al.* (2001) and Prop & Loonen (1989), who demonstrated that resources are not divided equally among flock members.

Both, the factorial models (Table 1) and the regression models (Table 2) indicate a strong effect of food quality on patch preference by Brent Geese. This result allows us to further elaborate upon the conceptual model put forward by Riddington *et al.* (1997). They found a preference of geese for short sward heights under unfertilised circumstances, because of a negative correlation between sward height and nitrogen content. Elimination of this correlation by fertilisation led to a preference for tall swards. Riddington *et al.* (1997) propose that intake rate of nitrogen is the criterion for geese to select patches. According to the concept of Riddington *et al.* (1997), the product of nitrogen and intake rate (nitrogen intake rate, mg N s^{-1}) has an optimum at intermediate sward height as a result of a decelerating functional response (Holling II, Holling 1959) and a declining quality of food. By fertilising the sward, this optimum disappeared under experimental conditions (Riddington *et al.* 1997). In that study, the main constraint for the geese was imposed by a limited intake rate at short sward heights. Our experiment was performed in the range of short swards, and we demonstrated that intake rate increased strongly with sward height. Still, we found a strong effect of forage quality rather than vegetation height. In our study, the levels of nitrogen differed by a factor two between fertilised and unfertilised treatments, while this difference was small in the experiment of Riddington *et al.* (1997) at low sward heights. So, as long as the differences in nitrogen content are large enough to discriminate between plots, Brent Geese respond to it, even when sward height is low. We thus support the hypothesis by Riddington *et al.* (1997) and Hassall *et al.* (2001) that both food biomass and quality determine patch choice in geese. The role of food biomass will become more prominent when variation in nitrogen content is small, as demonstrated by Hassall *et al.* (2001).

Stahl (2001) and Van der Graaf *et al.* (unpubl. data) report on experiments on salt marshes at Schiermonnikoog and along the Barnacle Goose flyway (Sweden, Russia) in which levels of biomass and quality were manipulated comparable to the present study. Their findings confirm that food quality affects patch choice in geese to a greater extent than food biomass. In addition facilitative and competitive interactions exist between the different species of herbivores on the marsh (Stahl 2001). Brent Geese were shown to prefer patches that had been previously grazed by Barnacle Geese with intermediate grazing pressure. Higher nutrient levels in these patches, in spite of lower biomass, may explain this reaction. High grazing pressures by hares, however, coincided with lower goose grazing pressure, presumably due to depletion effects (Stahl 2001, Kuijper 2004).

Food quality and intake rate

There is clear consensus about the decline of forage quality with increasing standing biomass (van Soest 1994, Wright & Illius 1995, Riddington *et al.* 1997). This phenological relationship has far reaching ecological consequences, given that herbivores are sensitive to even small differences in quality (Wilmshurst & Fryxell 1995, Wilmshurst *et al.* 1995, Hassall *et al.* 2001). Fryxell (1991) provided a model illustrating that ruminants benefit from aggregating at patches of intermediate biomass, because of a declining digestibility with higher densities of forage. Van de Koppel *et al.* (1996) showed that the density of small herbivores has an optimum at intermediate levels of standing biomass, where foraging efficiency is maximal. A decrease in foraging efficiency at high biomass may result from a lower food quality, or increased handling time and search effort caused by differences in sward structure (Van der Wal *et al.* 1998). Other factors may involve differences in vegetation composition or increased costs of locomotion and vigilance in taller swards. Our results provide an example of the concept outlined by Van de Koppel *et al.* (1996), and meanwhile point at the importance of nutrient intake rate rather than biomass intake rate alone. This is supported experimentally by field trials with captive Barnacle Geese and other waterfowl species, which clearly demonstrate that these small herbivores maximise intake rates of digestible nitrogen rather than dry matter intake rate (Durant *et al.* 2004). Therefore, small herbivores may choose to forage in areas of lower biomass because of higher nutrient intake rates that can be achieved there.

From patch to habitat use

The results of this experiment contribute to our understanding of the patterns of habitat use of avian herbivores. During spring large differences exist between habitats in timing of plant growth (Bakker *et al.* 1993) and nutritional quality of food plants (Bos & Stahl 2003). Through grazing, geese affect the growth stage of plants and forage quality (Ydenberg & Prins 1981 and Table 1). In time and space, spring staging areas of geese are therefore not homogeneous with respect to food quality (Van der Graaf *et al.* in press). Patch choice was demonstrated to be strongly affected by parameters of food quality (this experiment; Ydenberg & Prins 1981, Riddington *et al.* 1997). Declining nutrient intake rates with increasing levels of standing crop, for example, may explain observed patterns of habitat use within initially homogeneous agricultural grassland. In spring, the aggregation of Brent Geese on agricultural pastures leads to large differences in forage availability between areas with an intensively grazed short sward and areas with a tall sward that were left ungrazed (Spaans & Postma 2001). Field experiments using short-term exclosures supported the hypothesis that these patterns emerge because of declining nutrient intake rates with increasing levels of standing crop (Bos *et al.* 2004). In line with Hassall *et al.* (2001) and on basis of our new evidence, we conclude that food quality should be incorporated in models of habitat use for geese and other small herbivores.

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SAMENVATTING

Met behulp van veldexperimenten hebben wij het relatieve belang van biomassa en voedselkwaliteit voor de habitatkeuze van Rotganzen *Branta bernicla* bestudeerd. Het stikstofgehalte van de plant (een maat voor voedselkwaliteit) en de aanwezige hoeveelheid biomassa werden door middel van tijdelijke uitsluiting van begrazing en toevoeging van kunstmest onafhankelijk van elkaar gemanipuleerd. De voedselopnamesnelheid van wilde Rotganzen nam lineair toe met de hoogte van de grasmat. De aantrekkelijkheid van de experimentele veldjes voor wilde Rotganzen werd afgeleid uit de dichtheid van de ganzen op deze veldjes. De ganzen hadden de grootste voorkeur voor de plotjes met de hoogste stikstofgehaltes van de planten, en lieten zich daarbij niet meetbaar beïnvloeden door de voedselhoeveelheid. Begrazingsdruk, gemeten als het aantal keutels op een plot, liet hetzelfde patroon zien. We namen zelfs waar dat dominante paartjes bereid waren om de proefvlakjes met een goede voedselkwaliteit fél te verdedigen. Onze resultaten vullen eerdere studies (Riddington *et al.* 1997, Hassall *et al.* 2001, Durant *et al.* 2004) aan, doordat we kunnen laten zien dat voedselkwaliteit, zelfs op een korte grasmat, een belangrijke parameter is bij de habitatkeuze. Ze ondersteunen de stelling dat de opnamesnelheid van stikstof de habitatkeuze sterk beïnvloedt. Tenslotte biedt deze gedachtegang een verklaring voor het verspreidingspatroon van Rotganzen op agrarische graslanden in het voorjaar. (BIT)

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